



FREDERICK FROST BLACKMAN
JULY 25, 1866-JANUARY 30, 1947

IN MEMORIAM

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FREDERICK FROST BLACKMAN, M.A., D.Sc. (London), F.R.S., Fellow of St. John's College, Cambridge, and formerly Reader in Botany in the University of Cambridge, was born on July 25, 1866, and died at his home in Cambridge, England, on January 30, 1947, in his 81st year.

The name of F. F. BLACKMAN has long been familiar to every student of botany as one of the most distinguished plant physiologists of his time and he is assured of a permanent place in the history of that branch of botanical science to which he devoted his life and to which he, and the school of thought he founded and led, have contributed so much during the past half century or so. Although F. F. BLACKMAN spent the whole of his scientific career at Cambridge (entering as an undergraduate in 1887, appointed Demonstrator in Botany in 1891, and later serving as Lecturer and Reader from 1904 to 1936) his influence so permeates the development of plant physiology in his time that his story belongs in a measure to plant physiologists everywhere. He received the Fellowship of the Royal Society of London in 1906, was President of Section K (Botany) of the British Association in 1908, received other honors and distinctions including a Royal Medal of the Royal Society in 1926, and was President of the Section of Plant Physiology at the International Botanical Congress of 1930. Recognizing this, the American Society of Plant Physiologists elected him their first foreign Corresponding Member in 1932, and in 1934 awarded to him the Charles Reed Barnes Life Membership. Thus while Plant Physiologists everywhere take note of the passing of a great pioneer of their science, the AMERICAN SOCIETY OF PLANT PHYSIOLOGISTS is proud that he may be counted among its most distinguished members.

To appraise the work and influence of F. F. BLACKMAN one must look beyond the papers which bear his name, important as these were and are. His great contribution must be seen in perspective against the unfolding history of botany in his time. The strangely intermittent milestones in the early history of plant physiology in Britain are associated with particular names, familiar to every student, as those of NEHEMIAH GREW, STEPHEN HALES, JOSEPH PRIESTLEY, T. A. KNIGHT, and FRANCIS DARWIN. F. F. BLACKMAN, however, did something more over and above the discoveries identified with his name for he created the first school of plant physiology in England in the modern tradition. The significance of the life and work of BLACKMAN lies in the fact that he stimulated in England a new outlook on plant science as he led the way in applying quantitative experimental methods to the investigation of complex physiological processes and in for-

mulating interpretations through the application of physico-chemical reasoning.

In a measure BLACKMAN was the product of his time; his greatness lies in the fact that he responded to its challenge. The impetus of the great renaissance of biology as a practical laboratory science under Huxley at South Kensington in the 70's had been carried over into botany by THISELTON-DYER and by S. H. VINES. It is perhaps hard for contemporary teachers to appreciate that even in a country with such an ancient academic tradition as England, practical tuition in botany in the modern sense was unknown prior to the 70's, and plant physiology as a practical laboratory science literally did not exist. Drawing much of his stimulus from the great German physiologist SACHS, VINES was the first advocate of the new practical and experimental outlook on botany at Cambridge and in 1883 he was elected to the newly created post of Reader in Botany. VINES also compiled the first distinctively English textbook on the Physiology of Plants and seemed destined to found at Cambridge the School of Plant Physiology which did not come fully into being till later, for VINES left Cambridge in 1888 to become Professor of Botany at Oxford. The Readership as well as the fostering of the first practical teaching of Plant Physiology in the Botany School at Cambridge then devolved upon FRANCIS DARWIN. In the year 1881, as DR. F. F. BLACKMAN is quoted by F. O. BOWER as saying, "Plant Physiology may be said to have crystallized out in its pure form from the general solution of mixed botanical knowledge," for in this year the first edition of PFEFFER's textbook appeared. This was the plant physiological scene which awaited F. F. BLACKMAN. He was appointed Demonstrator under FRANCIS DARWIN in 1891 and later succeeded him to the Readership, a post he held until 1936 when he was in turn succeeded by one of his own colleagues and students, DR. G. E. BRIGGS.

Thus the life and active career of F. F. BLACKMAN spans almost the entire modern period of plant physiology in England. Due to his example and the prestige enjoyed by the school which grew up around him, Plant Physiology in England emerged as a branch of botanical thought and discipline worthy to take its place beside the more ancient and firmly established scientific traditions. We shall probably not see his like again for the historical setting which presented him with his opportunity and its challenge will not again return. For the high standards of scholarship which BLACKMAN maintained during this formative period, and the deliberate, calm judgment which pervaded his written works, the science owes him a deep debt of gratitude. Increasingly as the years passed, and until 1936, graduates and graduate students came to be influenced by his teachings, many of them destined to attain eminence and to occupy Botanical Chairs and official positions in England, the Dominions, and in the Empire. Thus it may be said that, from the turn of the century, F. F. BLACKMAN, as no other man, influenced the trend of the subject in the English speaking world.

BLACKMAN leaves no great textbook on the pattern of PFEFFER or SACHS. The actual physiological papers which bear his name are relatively few for so long and so important a career. Plant physiologists are likely to forget that in his earlier years BLACKMAN wrote with authority on the classification and phylogeny of the algae and this interest in algae overlapped the absorbing interest of his career in a discussion of "chromatic adaptation." However, two main series of papers reveal his physiological work and his influence even when he was not avowedly an author. The first of these series began with his own pioneer work and under the series title "Experimental Researches on Vegetable Assimilation and Respiration" appeared in twenty-one successive parts from 1895 to 1933. The other, entitled "Analytical Studies in Plant Respiration," appeared in seven successive parts from 1928 to 1937. These two series go far to tell the story of the Cambridge School of Plant Physiology under F. F. BLACKMAN and, insofar as he leaves a written legacy, we find it here. However, BLACKMAN was always deliberate in his writing and it is common knowledge in Cambridge and in England that much original work done at Cambridge during his period of tenure never reached the stage of publication. This loss to the larger community of plant physiologists can only be offset by the calm, matured judgment that pervades all the papers prepared under the influence of BLACKMAN's mind.

Reading his papers one is struck with the clarity of his formulations and his ability, where necessary, to rise above the tedious detail out of which great conclusions must often arise. Withal he maintained a dignity of style and language often lacking in our modern reporting of experimental findings and theoretical conclusions. In rereading these early works one comes unexpectedly across occasional touches which seem to carry down the years a breath of the Victorian and Edwardian England in which BLACKMAN moved and worked. His first published papers, communicated to the Royal Society of London by FRANCIS DARWIN in 1884, were really extended notes anticipating by a year in the Proceedings fuller presentations in the Philosophical Transactions. These notes and papers described "A New Method for Investigating the Carbonic Acid Exchange of Plants" and its application to an investigation "On the Path of Gaseous Exchanges between Aerial Leaves and the Atmosphere."

In this first work the method was one which was to be repeated several times as the long series unfolded. First a careful elaboration of a new technical procedure, with painstaking attention to detail, the technique was thoroughly evaluated and carefully described followed by the presentation, in an accompanying paper, of the mature investigation as it was finally carried out. For its time BLACKMAN's first apparatus was unusually elaborate, but he disarmingly states that: "Simplification of technique by complication of apparatus has been the guiding principle and the result is that, although the whole consists of at least eight separate pieces of apparatus, many of them being further in duplicate and all connected together by a

plexus of tubes, yet the working is so automatically arranged that the operator, beyond reading the burettes and occasionally working a finger bellows, has nothing to do but turn stopcocks."

BLACKMAN showed how by his new technique he could determine the carbon dioxide absorbed or released by a small area of a leaf surface or by a single seed and how he used the method to test whether gas exchange occurred through stomata or through the cuticle. Quantitative data were critically marshalled to show that both CO_2 evolved in the dark and assimilated in the light passed predominantly through the stomata. The cuticular theory had been advocated by BOUSSINGAULT who found that "leaves of *Nerium oleander* assimilated less when the upper stomatiferous surface had been coated with an unguent than when the lower stomatiferous surface had been so coated." BLACKMAN showed conclusively that BOUSSINGAULT's conclusion flowed from his use of such high concentrations of CO_2 (30%) that when this penetrated freely through the open stomata it inhibited assimilation whereas in the leaf with stomata almost completely blocked, the internal concentration still allowed assimilation to proceed.

The two subsequent papers in the series published in 1904-1905 recorded work of MISS MATTHAEI on the effect of temperature and illumination on the assimilation of carbon dioxide by leaves of cherry laurel (*Prunus lauro-cerasus*) and Jerusalem artichoke (*Helianthus tuberosus*). Here the emphasis was upon the interaction of the various factors which affect photosynthesis and upon the fact that under conditions of natural illumination it is the carbon dioxide concentration of the atmosphere which controls the rate of assimilation. Doubtless this phase of the work prompted BLACKMAN's most famous dictum, enunciated as the Principle of Limiting Factors in 1905 in the *Annals of Botany* (p. 289), in the following stately passage: "When a process is conditioned as to its rapidity by a number of separate factors the rate of the process is limited by the pace of the slowest factor"; and again, "When the magnitude of a function is limited by one of a set of possible factors, increase of that factor, and of that one alone, will be found to bring about an increase of the magnitude of the function." It matters little whether or not later investigators believe that the principle holds as rigidly as originally conceived. The importance of the principle so simply enunciated lies in the guidance it gave to the analysis and interpretation of experimental data obtained on systems upon which two or more variables interact.

It would be tedious to recapitulate the familiar trend of these researches. The series included papers by THODAY; with A. M. SMITH on photosynthesis in submerged aquatics; by BRIGGS, on the development of photosynthesis in seedlings (a subject studied earlier in BLACKMAN's laboratory with reference to etiolated seedlings by MISS IRVING); by WILMOTT, who elaborated and improved upon the familiar bubble counting technique with *Elodea*; by MASKELL, who investigated diurnal rhythm in the assimilation of leaves and made a critical study of assimilation in relation to stomatal opening;

by JAMES, who reinvestigated the dependence of photosynthesis upon carbon dioxide supply using submerged waterplants; and again by BRIGGS, upon the energetic efficiency of photosynthesis in green plants. BLACKMAN's recognition of slowly progressing thermal or "dark" reactions in photosynthesis which at high light intensity or high carbon dioxide concentrations cause the rate of the overall process to respond to temperature as do chemical reactions is acknowledged by the now general use of the term "Blackman Reaction" to describe this aspect of carbon assimilation.

Analytical studies in plant respiration opened with three papers; two in collaboration or association with PARIJA and one by F. F. BLACKMAN himself. The new series devoted a great deal of attention to the respiratory behavior of whole, stored apples and, later, of potatoes. The staple technique was again the determination of respired carbon dioxide. The time drifts in the respiratory behavior of stored apples were revealed as well as the changes which ensue when apples are transferred from air to oxygen or nitrogen. On this and similar evidence BLACKMAN formulated a general scheme of plant respiration and enunciated his concept of "Oxidative Anabolism." This was a device to explain the relation between the carbon dioxide evolved in air and in nitrogen. Accepting that the path of carbohydrate breakdown is probably common to both aerobic and anaerobic respiration (at least as far as three carbon intermediates), BLACKMAN postulated that in air part of these intermediates are metabolized to carbon dioxide and water and part resynthesized to products which become re-available for respiration. In nitrogen, on the contrary, the whole of the three carbon intermediates are utilized to form the products of fermentation. In this concept BLACKMAN followed, or was influenced by, the similar views expressed by MEYERHOF for muscle and yeast, though it must be confessed that the supporting body of biochemical evidence for the systems with which he was concerned was not strong. BLACKMAN's concept of "Oxidative Anabolism," like the MEYERHOF view, has not passed unchallenged and in particular its generality has been called into question. However, this brings BLACKMAN's contributions close to the more controversial fields of the present day. The practical science he did so much to foster has moved far from the days when exact measurements of overall gas exchange had yet to be made in order that the problems and processes of plant respiration and photosynthesis could be visualized. Other hands and minds must now thread the way through the often bewildering maze¹ of enzymes and substrates, coenzymes and cofactors, phosphorylations and dephosphorylations, and the sequence of interlocking cyclical processes which seem necessary to explain the biochemistry of these vital processes. F. F. BLACKMAN cleared the way for this task; it will be the simpler because he built so surely.

But what manner of man was F. F. BLACKMAN? Only those who enjoyed close contact with him are entitled to speak here though it is evi-

¹ What Blackman referred to in 1905 as "a congeries of enzymes, a colloidal honeycomb of katalytic agents. . . ."

dent that only a mind of great strength and a rare spirit could have exerted so profound an influence over the long succession of students, collaborators, and colleagues. Perhaps we may be permitted to quote from one who knew him and who writes: "He lived a full and balanced life; his devotion to science did not prevent him from cultivating other interests which included music, architecture, and painting. To problems in all spheres BLACKMAN brought a calm and dispassionate mind and a habit of careful and patient discrimination. There was an unobtrusive strength in his personality which seemed to derive from the blending of wisdom, subtlety of perception and gentleness.

"BLACKMAN was a great teacher as well as a gifted investigator and he linked closely together the two functions of teacher and research. His advanced lectures were based largely upon experimental results obtained in his own school and many of these were (and still remain) unpublished. Each lecture was a perfect presentation in which BLACKMAN succeeded in imparting to his hearers a point of view as well as an ordered array of facts illustrating a particular theme. To attend his lectures was a privilege never to be forgotten and an experience which formed an important part of the discipline of the school of research which grew up under his inspiration."

The AMERICAN SOCIETY OF PLANT PHYSIOLOGISTS therefore joins with botanists and plant physiologists everywhere and pays its tribute to the memory of DR. F. F. BLACKMAN, a great pioneer in the modern experimental approach to the study of plants and plant behavior.

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